Light enough to travel or wise enough to stay? Brain size evolution and migratory behaviour in birds

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Abstract

Brain size relative to body size is smaller in migratory than in non-migratory birds. Two mutually non-exclusive hypotheses had been proposed to explain this association. On the one hand, the 'energetic trade-off hypothesis' claims that migratory species were selected to have smaller brains because of the interplay between neural tissue volume and migratory flight. In contrast, the 'behavioural flexibility hypothesis' argues that resident species are selected to have higher cognitive capacities, and therefore larger brains, to enable survival in harsh winters, or to deal with environmental seasonality. Here, I test the validity and setting of these two hypotheses using 1,466 globally distributed bird species. First, I show that the negative association between migration distance and relative brain size is very robust across species and phylogeny. Second, I provide strong support for the energetic trade-off hypothesis, by showing the validity of the trade-off among long-distance migratory species alone. Third, using resident and short-distance migratory species, I demonstrate that environmental harshness is associated with enlarged relative brain size, therefore arguably better cognition. My study provides the strongest comparative support to date for both the energetic trade-off and the behavioural flexibility hypotheses, and highlights that both mechanisms contribute to brain size evolution, but on different ends of the migratory spectrum.

Introduction

Brain size relative to body size has long been considered a major determinant of the cognitive abilities of a given individual, or species (Sol 2009). For instance, large relative brain size has been linked to a wide range of benefits, including increased survival, adaptability to novel environments, innovation propensity, variability of habitats occupied, invasiveness and sociability (Lefebvre et al. 2004, Lefebvre and Sol 2008, Sol 2009, Sol et al. 2007, 2010, Lefebvre 2013). Nevertheless, in spite of the multifaceted benefits conferred by a large brain (relative to body size), there is a downside: high metabolic cost (Sol 2009, Isler and van Schaik 2009). The brain is one of the most energetically expensive organs in the body, consuming up to ten times more energy per unit mass than skeletal muscle (Isler and van Schaik 2006, 2009). Therefore, relative brain size in a given species should reflect a careful balance between costs and benefits; the evolutionary optimum should be the size that maximises survival and reproductive success as a function of species ecology, life history, and behaviour (Sol et al. 2010).

One major ecological constraint on relative brain size across flying homothermic vertebrates is distance travelled during migration (Winkler et al. 2004). This association has repeatedly been demonstrated at the species level in birds (e.g. Winkler et al. 2004, Sol et al. 2005, Vincze et al. 2015), and bats (McGuire and Ratcliffe 2011), as well as at the subspecies level in birds (Cristol et al. 2003, Pravosudov et al. 2007, Fuchs et al. 2015). The correlation is very robust and, in all cases, relative total brain weight decreases with increasing migration distance (Cristol et al. 2003, Winkler et al. 2004, Sol et al. 2005, Pravosudov et al. 2007, McGuire and Ratcliffe 2011, Vincze et al. 2015). The two hypotheses proposed to explain this association are, by definition, explaining variation on two different ends of the migratory distance spectrum (i.e. residents vs. long-distance migrants).The energetic trade-off hypothesis builds upon the metabolic costs of migration, and that of developing and sustaining neural tissues, suggesting energetic conflict between these two demands (Winkler et al. 2004, McGuire and Ratcliffe 2011). Migration is one of the most energetically challenging periods in a bird's life: Bar-tailed Godwits (*Limosa lapponica*), for example, cover 11,000 km in a single non-stop flight (Gill et al. 2009). Such strenuous movements are often on the edge of avian physiological endurance and necessitate a range of adaptations to make the journey possible (Hedenström 2010). For instance, we know that body mass is often doubled during the pre-migratory fattening process to support the

energetic needs of the journey (Newton 2008), while almost all organs undergo significant size reduction prior to migration to minimise the metabolic cost of transport (Piersma and Lindström 1997, Battley et al. 2000). An extensive study on the morphological adaptations to migration in birds found that heart size, the most calorie-hungry structure in the body, is relatively smaller in long-distance migrants (Vágási et al. 2016), corroborating negative selection on energetically expensive organ sizes. Given the energetic cost of flight, long-distance migration may compromise a bird's ability to support the high metabolic cost of a large brain. Thus, the energetic trade-off hypothesis predicts directional selection that favours smaller relative brain size with increasing migration distance.

In contrast, the behavioural flexibility hypothesis assumes a positive directional selection on relative brain size in resident birds (Winkler et al. 2004) instead of negative selection in migrants. Resident bird species often experience strong spatial and temporal fluctuations in their environments, and therefore tend to rely more heavily on novel food sources, exploited through innovations and learning (Sol et al. 2005, Aplin et al. 2013). Classical examples of such behaviours are the 'milk bottle' innovation in Blue Tits (*Cyanistes caeruleus*) (Aplin et al. 2013), or Great Tits (*Parus major*) predating on hibernating bats (Estók et al. 2009). Such behaviours usually only happen under environmental conditions (e.g. harsh winters) that limit normal food sources (Estók et al. 2009); this also highlights the importance of innovation in seasonal and harsh environments. Indeed, innovation propensity and associated relative brain size (Timmermans et al. 2000, Reader and Laland 2002), are both highest in resident species and lowest in long distance migrants (Sol et al. 2005). Nonetheless, whether higher degrees of innovation in resident species reflects necessity, or their capacity, has yet to be determined. To attempt to address this, a reformulation of the behavioural flexibility hypothesis by inverting causalities was coined the 'migratory precursor hypothesis' (Sol et al. 2005). The elevated cognitive capacity of large-brained birds would enable them to be residents, while small-brained species are forced to migrate. Irrespective of causality, higher cognitive needs, especially if innovative behaviour is socially transmitted (Aplin et al. 2013), may represent one plausible explanation for the larger relative brain sizes of resident bird species and might represent a coping mechanism to harsh or seasonal environments.

Exploring the relationship between relative brain size and the environmental harshness, or variability, experienced by resident birds in different climatic zones, or latitudes, could provide a strong test of the

behavioural flexibility/migratory precursor hypothesis (Winkler et al. 2004). Studies investigating the behavioural flexibility hypothesis to date are, however, scant and results are contradictory (Schuck-Paim 2008). In neotropical parrots, climate variability was shown to be positively associated with relative brain size (Schuck-Paim 2008), which provides some intraspecific support for the behavioral flexibility hypothesis. Moreover, elevated winter harshness and the associated increased requirement for food-caching is correlated with enlargement of brain regions responsible for spatial memory in different Black-capped Chickadee (*Poecile atricapillus*) populations (Roth and Pravosudov 2009, Roth et al. 2011). There is thus some evidence that the environmental harshness and fluctuation influence brain evolution and functionality; however, which aspects of the environment are most important in this respect, and in what settings do selective forces act, remain unanswered. By extending the geographical and taxonomic coverage of previous studies, and by testing how different environments experienced by species with similar migratory behaviours result in relative brain size differentiation could provide potential answers to these questions.

In this study, I test separately the validity of the energetic trade-off and behavioural flexibility hypotheses, and explore the nature of the negative correlation between relative brain size and migratory behaviour in birds. First using data from the literature, I assess the generality of this negative association on the basis of an extensive list of bird species (n = 1,466), across a very wide body size (2.7 g - 44kg) and taxonomic range, encompassing ratites to passerines. Second, using migration measured on a continuous scale (0 km – 13,063 km) and species with migration distance > 0 km (i.e. excluding residents), I test the validity of the energetic trade-off hypothesis. This hypothesis will gain support if there is a negative association between migration distance and relative brain size, and the effect will be strongest among long-distance migratory birds. Third, using only resident species (n = 937), across a tropical-to-arctic distributional spectrum, I test the validity of the behavioural flexibility hypothesis. In this final case, I use winter minimum temperature, seasonality of ambient temperature, and wintering latitude to test which one of these factors best predicts the relative brain size of resident birds. The behavioural flexibility hypothesis will be supported in cases where relative brain size increases with latitude or seasonality, or decreases with increasing winter minimum temperature; note that the latter ought to have the strongest effect when the nature of this association is defined by environmental harshness. My study thus provides the first broad and fine scale mutual test for the

behavioural flexibility and energy trade-off hypotheses, to explore how these mechanisms shape the evolution of avian brains.

Materials and Methods

BRAIN AND BODY SIZE

I extracted brain and body weight data from Iwaniuk and Nelson (2003), a primary dataset listing the endocranial volumes of a wide range of birds. Endocranial volume is a highly reliably method to measure brain size both across, and within, species (Iwaniuk and Nelson 2002). Brain mass was then obtained by multiplying reported endocranial volumes by the density of fresh brain tissue, 1.036 g/mL (Iwaniuk and Nelson 2003), and the dataset was then further modified by calculating a single mean for species for which data was originally reported at the subspecies level (e.g. *Platycercus elegans elegans* and *P. e. flaveoulus*), or using two synonymous names (e.g. *Esacus magnirostris* and *E. neglectus*). In these cases, species means were calculated as the weighted arithmetic mean of separate measurements where weights were represented by the number of specimens measured in each case.

Given that larger-bodied species have larger brains, body mass needs to be controlled for when comparing brian sizes across species (Lashley 1949). Body mass was therefore included in each of the models presented here, as brain size relative to body size is a measure that reflects the surplus of neural tissue versus the amount required for basic bodily functions (Lashley 1949), and is associated with a range of cognitive traits across species (see above).

MIGRATION DISTANCE

Distribution maps (shape files) for each species were downloaded from http://www.birdlife.org/datazone/info/spcdownload (BirdLife International and NatureServe 2014), and the geometric centroid of the spatial polygon of breeding (breeding and resident) and wintering (wintering and resident) ranges were calculated using the ‘gCentroid’ function in the R package ‘rgeos’ (Bivan and Rundel 2013). Migration distance was calculated as the geographic distance between breeding and wintering centroids using a custom function written in R (Vágási et al. 2016). ‘Migratory distance’ thus denotes the average distance travelled by a given species during migration. Additionally, I extracted the latitude of the non-breeding centroids, and calculated absolute values (thereafter, 'non-

breeding latitude').

ENVIRONMENTAL HARSHNESS AND SEASONALITY

I extracted ambient temperature data from the University of East Anglia Climate Research Unit database (CRU, http://www.cru.uea.ac.uk/; version 3.10.01; Mitchell and Jones 2005), a global dataset containing interpolated monthly average land temperatures (°C) from 1901 onwards in a grid of spatial coordinates (0.5 × 0.5 degrees). I used the most recent temperature data ('cru_ts_3.23.2011.2014', downloaded on 26 September 2015) comprising monthly temperature means from 2011 to 2014. First, I averaged these four years to calculate mean monthly temperatures for each spatial grid cell. From the resulting data file, I created a 12-layer shape file, where each layer contained a month's mean temperature separately for each cell. Third, by intersecting temperature and species distribution shape files, I calculated the monthly mean temperatures for each species, separately for their wintering and breeding grounds. This resulted in 12 monthly means on the breeding ground, and 12 monthly means on the wintering ground for each species. For the wintering ground, I extracted the lowest monthly mean (thereafter, 'non-breeding minimum temperature') as a proxy of winter harshness. 'Seasonality' was calculated as the difference between the lowest and highest monthly mean temperatures on the breeding ground, and thus it reflects the extent of maximum thermal fluctuation during the course of a year on the breeding ground for each species. Note that neither non-breeding minimum temperature nor seasonality reflects the true environmental conditions experienced by species with migration distances greater than 0 km. This is so, because long-distance migrants often do not experience the coldest periods on the wintering grounds (e.g. July in South-America for White-rumped Sandpiper *Calidris fuscicollis*), nor do they on the breeding grounds (e.g. January in North-America for the same species). The latter is true for short-distance migrants too, due to their migratory tendencies under harsh environmental conditions., Therefore, both non-breeding minimum temperature and seasonality were only used in models based on species that have a migration distance of less than 1,000 km; the true values of non-breeding minimum temperature and seasonality experienced by long distance migrants could not be calculated due to lack of information on their temporal migratory patterns. In addition, because non-breeding minimum temperature and seasonality could not be calculated for three fully resident species with extremely restricted distributions (i.e., *Anas laysanensis, Porzana atra*, *Vini stepheni*), sample size slightly varies between models with different explanatory variables.

PHYLOGENY

In order to implement the similarity of species due to common descent, I controlled for phylogenetic relatedness in all analyses. To do this I downloaded 100 random trees from www.birdtree.org (Jetz et al. 2012) using the Hackett backbone tree (Hackett et al. 2008), and repeated every model with each of these random trees to control for phylogenetic uncertainty (Rubolini et al. 2015).

STATISTICAL ANALYSES

I performed phylogenetic generalised least squares regressions (PGLS) using the 'pgls' function as implemented in the R package 'caper' (Orme et al. 2013). Brain size was used as a dependent variable in double predictor models, containing body mass and one of the following covariates: migration distance, non-breeding minimum temperature, seasonality or non-breeding latitude. To test for the energetic trade-off hypothesis, I built double predictor models containing migration distance and body mass as explanatory variables on subsets of species over seven different migration distance intervals (i.e. migration distance $\geqslant$0 km, >0 km, >500 km, >1,000 km, >2,000 km, >0 km & <500 km, >500 km & <1,000 km). However, because the effect of migration distance might be confounded by the effect of climate, given that these two often covary (i.e. species with longer migration distances experience milder wintering climates), I repeated the above model using a subset of species with migration distance >2,000 km, and with non-breeding range centroids within the tropics (23.4°N-23.4°S). I expect the strongest effect of migration distance on brain size in species with the longest migratory trajectories if the energetic trade-off hypothesis is to be supported. Further, to test the behavioural flexibility hypothesis, I built double predictor models containing body mass and non-breeding minimum temperature, seasonality or non-breeding latitude, as explanatory variables on subsets of species with five different migration distance intervals (i.e. migration distance = 0 km, <500 km, <1,000 km, >0 km & <500 km, >500 km & <1,000 km). I expect the strongest effect of all three variables in fully resident species, and that the strength of these associations will decrease with the length of migration distance.

All the above analyses were repeated using passerines only, since these perching songbirds (order Passeriformes) are less variable morphologically and trace their origins to a more recent common

ancestor than the non-passerines, but are more speciose and exhibit an impressive array of cognitive abilities and migratory strategies (Sol et al. 2005). Moreover, models were repeated using non-passerine bird orders with sufficient number of species and with considerable variance in the focal explanatory variable. These orders were the *Anseriformes* and *Charadriiformes* for the energetic trade-off hypothesis and *Piciformes*, *Strigiformes* and *Galliformes* for the behavioural flexibilty hypothesis. Taxonomic order was obtained using the 'tax_name' function as implemented in the R package 'taxize' (Chamberlain et al. 2014), and each of the models described above was repeated with 100 random phylogenetic trees; AICc scores extracted and AICc weights were calculated. AICc weights were then used to calculate weighted mean t and p-values across the 100 models; distributions of both t and p values of the focal explanatory variables in these model sets were plotted and are reported in Supporting Information S1 (Table 1), and Supporting Information S2a and S2b (Table 2) for the entire species and passerines respectively. Phylogenetic dependence was estimated using Pagel's λ, set to the most appropriate value assessed by maximum likelihood in each model. Brain mass and body mass were log-transformed prior to analyses, all other variables were used untransformed.

Migratory species often accumulate large amounts of fat to support their migratory flights (Newton 2008). Such body mass fluctuations might bias the results of brain size analyses in cases where migratory species have larger body masses recorded in the dataset due to accumulated fuel reserves. In these cases, relative brain size in longer distance migrants (with more fuel accumulated) would be estimated erroneously as smaller. To rule out this confounding effect, I first tested whether mean body mass used in the brain size models is correlated with migration distance (n = 1,466). Second, I obtained data on minimum and maximum body mass from Dunning (2008) for 1,131 bird species present in the brain dataset. Minimal and maximal body masses were obtained by averaging sexes, subspecies, and populations if separate values were available, and on the basis of these data I tested whether the ratio between minimum and mean body mass, as well as the ratio between maximum and mean body mass covaries with migration distance. All three of these models were tested in a PGLS framework, using 100 phylogenetic trees. Results reported are weighted means (by AICc weights) of t- and P-values calculated across the 100 models. Model averaging was performed in the same fashion as with brain size models, and mean body mass and the two body mass ratios were all log-transformed prior the analyses.

Graphical presentation of data was done using residual brain masses, calculated form a log-log standard linear regression between brain mass and body mass. Fitted lines and associated standard errors were obtained from the PGLS model between the residual brain mass and the focal predictor variable, and standard errors were obtained using the 'predictSE.gls' function as implemented in R package 'AICcmmodavg' (Mazerolle 2015). P values were not adjusted for multiple comparison, in order to avoid inflation of the type II error probability (Rothman 1990, 2014). All statistical analyses and graphical representations of results were carried out in R 3.2.0 (R Core Team 2015) and all data used in the analyses are reported in Supporting Information S4.

Results

DATA-SET COVERAGE

Across the dataset (Fig. 1), migration distance varied from 0 km (n = 937 species) to 13,063 km in the White-rumped Sandpiper (*Calidris fuscicollis*), while non-breeding latitude varied from 74.61° in the Ivory Gull (*Pagophila eburnea*) to 0.01° in the Spot-winged Antbird (*Schistocichla leucostigma)*. In species with migration distance <1,000 km, non-breeding minimum temperature ranged from –29.05°C in the Rock Ptarmigan (*Lagopus muta*) to 26.84° C in the Northern Screamer (*Chauna chavaria*), while seasonality varied from 0.42°C in the Eyebrowed Jungle-flycatcher (*Rhinomyias gularis*) to 44.75°C in the Asian Rosy Finch (*Leucosticte arctoa*).

THE ENERGY TRADE-OFF HYPOTHESIS

Brain size is strongly negatively correlated with migration distance across the entire migratory spectrum (Table 1, Fig. 2A,D). This association disappears when fully resident species (migration distance = 0 km) were excluded from analyses (Table 1). Indeed, when analyses were restricted to short distance migrants (0 - 1,000km), the negative association between brain size and migration distance did not emerge (Table 1, Fig. 2B,E) indicating that short distance migrants do not fit the relative brain size – migration distance continuum when this is assessed using the entire migratory spectrum. Nevertheless, the strength of the negative association between brain size and migratory distance increased again, despite a reduction in sample size, after short-distance migrants were excluded (i.e. subsets with migration distance from >500 km to >2,000 km, Table 1 and Fig. 2C,F). The negative

association between migration distance and brain size was also strong for the subset of species with tropical wintering centroids and migration distances over 2,000 km. All results were highly consistent when repeated just for passerines (Table 1, Fig. 2). Similar pattern was found in the case of *Charadriiformes* and *Anseriformes*, but these associations did not reach significance (Supporting Information S3, Table S1, Figure S1).

Mean body mass is negatively associated with migration distance (PGLS, n = 1,466, t = -2.25, p = 0.0035), indicating that longer distance migratory species have lower, not higher, average body masses than species with shorter migratory distances. The ratio between minimum and mean body mass decreased slightly with migration distance (PGLS, n =1,131, t = -2.54, p = 0.0120), while the ratio between maximum and mean body mass was strongly positively associated with migration distance (PGLS, n =1,131, t = 3.42, p = 0.0008).

THE BEHAVIOURAL FLEXIBILITY HYPOTHESIS

Non-breeding minimum temperature has a strong effect on brain size in both fully resident and short-distance migratory species (Table 2, Fig. 3); the lower the non-breeding minimum temperature, the larger the brain size (Table 2 and Fig. 3). Indeed, the effect of non-breeding minimum temperature was comparable across different migratory intervals between 0 and 500 km, but not above 500 km (Table 2). In several species subsets, non-breeding minimum temperature is the only significant predictor of relative brain size, while seasonality and non-breeding latitude have little predictive power. Where significant, brain size increases with seasonality and increases with increasing non-breeding latitude (Table 2); all results were highly consistent when repeated using just passerines (Table 2). Moreover, results were highly consistent for the *Piciformes* and the *Strigiformes* bird orders, but none of the tested environmental variables influenced brain size in the *Galliformes* bird order (Supporting Information S3, Table S2, Figure S2).

Discussion

In this study, I show in the first place that whole brain size in birds is negatively correlated with migration distance. This key result corroborates earlier studies (Sol et al. 2005, 2010, McGuire and

Ratcliffe 2011), but extends this negative correlation across much wider taxonomic and geographic scales, and provides a basis for the generalisation of this association outside passerines. Secondly, my study provides strong and clear support for the validity, and context, of the two alternative hypotheses explaining the association between brain size and migration distance in birds, the energetic trade-off and the behavioural flexibility hypotheses.

ENERGETIC TRADE-OFF HYPOTHESIS

Relative brain size in birds strongly decreases with increasing migration distance; this is true when considering the entire migratory spectrum, or just long-distance migrants. First, results based on the entire migratory spectrum corroborate earlier studies (Sol et al. 2005, 2010, McGuire and Ratcliffe 2011), and provide a basis for generalising the negative association between relative brain size and migration distance across all birds. Note however, that the negative association between brain size and migration distance was not significant in the two non-passerine bird orders tested, however both of these shower similar patterns. Second, results based just on long-distance migrants provide the strongest support yet for the energetic trade-off hypothesis, indicating that it exists not just among major migration distance subdivisions (e.g. residents, short-, and long-distance migrants), but also on a fine scale within just long-distance migrants. One major drawback of earlier studies is that they categorised species based on the length of their migratory trajectories; long-distance migrants were handled within just one (Sol et al. 2005, McGuire and Ratcliffe 2011), or few categories (Sol et al. 2010). Here, I provide support for the energetic trade-off hypothesis by exploring fine-scale variations of both migration distance and relative brain size within these categories, and results show that short-distance migrants do not fit on the relative brain size – migration distance linear continuum. This suggests that two different mechanisms control the evolution of the disparate relative brain sizes found in migrants and residents, and that these mechanisms act on separate ends of the migratory spectrum. In resident birds it is cognitive needs, while in migrants, energetic limitations appear to be important in regulating brain size evolution. Results suggest that shorter-distance migrants are only partially affected by both of these mechanisms.

Due to the correlative nature of this study, the negative association between migration distance and relative brain size could potentially be confounded by several factors. First, the longer the migration

distance, the milder wintering conditions can get; therefore, the smaller brain size in long-distance migrants could also be explained by the year-round milder environment these birds experience. Note however that the negative association between brain size and migration distance is also apparent in species with migration distances over 2,000 km, and with wintering range geometric centroids within the tropics. This result suggests that the negative association between brain size and migration distance is unlikely to be confounded by correlated climate effects, and that the nature of this association is indeed an energetic trade-off. Second, given that migratory species often accumulate large fat reserves to support their migratory flight, relative brain size might be underestimated if lean body mass is overestimated in migrants. Such errors in the data could lead to a false identification of the energetic trade-off hypothesis as true, given that larger fuel amounts are accumulated in longer distance migrants. Note however, that mean body mass used in the analyses was actually negatively correlated with migration distance in this dataset, indicating the migratory fuelling did not affect mean body mass estimates used here. Additionally, for a subsample of species (n = 1,131) the ratio of minimum to mean body mass decreased slightly with increasing migration distance. This weak association, compared to the strong positive association between migration distance and the ratio of maximum to mean body mass indicates that migratory fuelling is unlikely to largely distort mean body mass values used here and is therefore unlikely to confound my results.

An earlier phylogenetic path analyses showed that the largest fraction (68%) of the correlation between relative brain mass and migratory distance is a direct effect of migration on brain size (Sol et al. 2010). Although these authors argued that brain size reduction in migrants could have originated from the lowered importance of cognitive capacities in these birds (Sol et al. 2010), relative brain size in short-distance migrants is not affected by migration distance. This result is important because cognitive needs for resource exploitation in short-distance migrants might arguably be closer to those of long-distance migrants than to those of residents simply because of their migratory tendencies in case of resource shortages and their potentially decreased needs for innovation (e.g. irruptive or facultative migration, Newton 2008). Therefore, it is unlikely that the brain size of long-distance migrants shrinks simply because of a reduction in cognitive need, leaving the energetic trade-off hypothesis as a more plausible explanation. This is especially the case given that the negative association between migration distance in long-distance migratory species (over2,000 km) and with tropical non-breeding ranges still holds

true, although cognitive needs within this group of birds could potentially be similar. Second, given that migration is an extremely strenuous activity (Hedenström 2010), and the length of migration distance was shown to negatively correlate with the energetically expensive heart size (Vágási et al. 2016), I consider the pure energetic trade-off hypothesis to be the most likely explanation of brain size reduction in long-distance migrants.

THE BEHAVIOURAL FLEXIBILITY HYPOTHESIS

Non-breeding minimum temperature is a strong predictor of relative brain size in fully resident (n = 934 species), and short-distance (up to 500 km, n = 142 species) migratory birds. In other words, the colder the minimum monthly temperature on the wintering ground the larger the relative brain size of birds. Additionally, relative brain size significantly increased with non-breeding latitude and seasonality although these effects are weaker than the association with non-breeding minimum temperature. Thus, my results strongly indicate that winter harshness is associated with larger brains across the avian phylogeny. Given that non-breeding latitude and seasonality have weaker effects than non-breeding minimum temperature on relative brain size, it is more likely that environmental severity reflected by low ambient temperature, high snow cover, and/or reduced day length (Roth and Pravosudov 2009), rather than the seasonal nature of the environment being the strongest selective force on brain size evolution in resident birds. Indeed, the importance of climate severity in brain evolution has previously been reported; food- caching Black-capped Chickadees from harsher wintering ranges have better spatial memory, as well as larger hippocampi and higher neuronal density in these brain regions responsible for this skill (Roth and Pravosudov 2009, Pravosudov and Clayton 2002, Roth et al. 2011). Enhanced spatial memory is thus a potential mechanism enabling birds to cope with environmental harshness, especially in food-caching species. The hippocampus occupies just a small part of total brain volume, however, and thus the results presented here must reflect additional neural adaptations to environmental severity. To date we have very limited knowledge on how environmental conditions, in particular which aspects of the environment and in which way does it influence brain and cognitive evolution across species. The topic therefore deserves considerable future scientific attention.

FURTHER REMARKS

Change in the size of different brain regions with migration distance is non-uniform (McGuire and Ratcliffe 2011, Fuchs et al. 2014, Vincze et al. 2015), and reduction of whole brain size with increasing migration distance is mostly accounted for by reduction in the size of the telencephalon (Vincze et al. 2015), the center of higher cognitive processes. In line with the latter results, Fuchs et al. (2015) found that migratory lark sparrows (*Chondestes grammacus*) showed a clear trend toward having larger nidopalliums (a central neural substrate of higher cognitive processes in birds) than residents of the same species. Therefore, it is probable that the larger relative brain size of resident birds compared to migrants is indeed associated with their larger telencephalon and better cognitive abilities that could enhance their survival probability especially under harsh environmental conditions. It would be insightful then to consider how environmental harshness in various resident birds influences the evolution of different brain regions, on a cross-species scale. Such a follow-up study could provide more precise insights into whether increase in the size of telencephalon (and regions thereof, e.g. hippocampus) is specifically selected in species wintering under harsher environmental conditions. Additionally, whether brain size enlargement preceded, or followed, the switch in migratory habit in avian evolution is yet to be determined. Pravosudov et al. (2007) for instance examined three subspecies of white-crowned sparrow (*Zonotrichia leucophrys*) and showed that it is more likely that brain size enlargement took place after the switch from migratory to sedentary behaviour. Nonetheless, further studies should examine the nature if these associations on a broader taxonomic scale.

Relative brain size variation is subtler in bats than in birds (McGuire and Ratcliffe 2011), and the authors suggest that this discrepancy could originate from the shorter migration distances covered by bats relative to birds. In addition, I suggest that besides the longer migration distances selecting for smaller brains in both birds and mammals, harsh environments experienced by vigilant resident birds (but not hibernating resident bats) will select for enlarged brains, further distancing relative brain volume of resident from that of long-distance migratory birds.

Here I show that both environmental harshness and migration distance strongly affect brain size evolution in birds. It's important to note however that these two factors appear to explain only a fraction of the cross-species variance observed (see Fig 2,3). The extra variation is certainly explained by other social, ecological, physiological or life-history factors not examined here that affect brain or

cognitive evolution across birds.

Importantly, comparative studies of full brain size have been subject to strong criticism in recent years (Healy and Rowe 2007). The argument is that the brain is responsible for a wide range of functions, therefore is not suitable to directly associate it with specific behaviours. However, a range of studies indicate that relative brian size is a strong predictor of cognitive abilities, such as innovativity, learning, invasion, tool use, memory, variability of habitats occupied (Schuck-Paim 2008, Sol 2009, Sol et al. 2007, 2010). Moreover, recent comparative evidence reveals that large brains in birds are a result of disproportionately enlarged pallial areas known to play key roles in avian cognition (Sayol et al. 2016). These studies suggest that whole brain size is indeed a useful tool of assessing general evolutionary patterns of brain and cognitive evolution. The results obtained this way will naturally benefit from a more specific research framework, where the change in specific brain regions is precisely assessed.

CONCLUSIONS

Here I demonstrate that increasing environmental harshness during the non-breeding period is associated with larger relative brain sizes in both resident and short distance migrants and thus, in these species, selection for behavioural flexibility must be an important driver of brain size evolution. Nevertheless, because I also show that increasing migration distance is linked with decreased relative brain size, the energetic trade-off hypothesis is also supported, especially in species with long migratory flights. Taken together, this study illustrates that the selection for larger brain size by cold wintering temperatures and the selection for smaller brain size by migratory flight both contribute to the evolution of disparate relative brain sizes of migratory and resident bird species, and these two mechanisms act on different ends of the migratory spectrum. Finally, it is important to note that I have taken a correlative approach here, therefore the nature of causalities cannot be inferred from my results. In other words, migratory habit or geographic distributions may select for larger or smaller brains, but brain size evolution might as well precede switch in migratory strategy or define suitable distribution ranges (Sol et al. 2005, Pravosudov et al. 2007).

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SUPPORTING INFORMATION

Supporting Information S1: These figures represent parameter distribution over 100 models with different phylogenetic trees. Each row of the figure represents a row from Table 1. The first two columns represent t- and P-values from models of the entire species pool, while the other two from models of Passerines.

Supporting Information S2: These figures represent parameter distribution over 100 PGLS models with different phylogenetic trees. Each row of the figure S2a represents a row from the first part of Table 2 (i.e. entire species pool), while S2b from the second part of Table 2 (i.e. *Passerines*). 1St and 2nd columns represent parameters from models containing non-breeding minimal temperature, 3rd and 4th columns from models containing seasonality, 5th and 6th columns from models containing non-breeding latitude.

Supporting Information S3: Models exploring the relationship between brain size and migration distance (in two non-passerine bird-orders) as well as with non-breeding minimal temperature, seasonality and non-breeding latitude (in three non-passerine bird orders). Results of models and graphical presentation are both given.

Supporting Information S4: Data used in the analyses.

LITERATURE CITED

Aplin, L. M., B. C. Sheldon and J. Morand-Ferron. 2013. Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. Anim. Behav. 85:1225-1232.

Battley, P. F., T. Piersma, M. W. Dietz, S. Tang, A. Dekinga and K. Hulsman. 2000. Empirical evidence for differential organ reductions during trans–oceanic bird flight. Proc. R. Soc. Lond. B

267:191-195.

Bartoń, K. 2015. MuMIn: Multi-Model Inference. R package version 1.15.1. http://CRAN.R-project.org/package=MuMIn

BirdLife International and NatureServe. 2014. Bird species distribution maps of the world. BirdLife International, Cambridge, U.K.

Bivand, R. and C. Rundel. 2013. Rgeos: Interface to Geometry Engine - Open Source (GEOS). R Package Version 0.3-2.

Chamberlain, S., E. Szocs, C. Boettiger, K. Ram, I. Bartomeus and J. Baumgartner. 2014. taxize: Taxonomic information from around the web. R package version 0.3.0. https://github.com/ropensci/taxize

Cristol, D. A., E. B. Reynolds, J. E. Leclerc, A. H. Donner, C. S. Farabaugh and C. W. S. Ziegenfus. 2003. Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than non-migratory conspecifics. Anim. Behav. 66:317–328.

Estók, P., S. Zsebők and B. M. Siemers. 2009. Great tits search for, capture, kill and eat hibernating bats. Biol. Lett. 6:59–62.

Fuchs, R., H. Winkler, V. P. Bingman, J. D. Ross and G. Bernroider. 2014. Brain geometry and its relation to migratory behavior in birds. J. Adv. Neurosci. Res 1:1-9.

Fuchs, R., V. P. Bingman, J. D. Ross and G. Bernroider. 2015. Brain contrasts between migratory and nonmigratory North American lark sparrows (Chondestes grammacus). NeuroReport *26:*1011-1016.

Gill, R. E. Jr., T. L. Tibbitts, D. C. Douglas, C. M. Handel, D. M. Mulcahy, J. C. Gottschalck, N.Warnock, N. J. McCaffery, P. F. Battley and T. Piersma. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc. R. Soc. Lond. B 276:447–457.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K. L. Han, J. Harshman et al. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

Healy, S. D. and C. Rowe. 2007. A critique of comparative studies of brain size. Proc. R. Soc. Lond. B 274:453-464.

Hedenström, A. 2010. Extreme endurance migration: what is the limit to non-stop flight. PLoS Biol,

8:e1000362.

Isler, K. and C. van Schaik. 2006. Costs of encephalization: the energy trade-off hypothesis tested on birds. J. Hum. Evol. 51:228-243.

Isler, K. and C. P. van Schaik. 2009. The expensive brain: a framework for explaining evolutionary changes in brain size. J. Hum. Evol., 57:392-400.

Iwaniuk, A. N., and J. E. Nelson. 2002. Can endocranial volume be used as an estimate of brain size in birds? Can. J. Zoolog. 80:16-23.

Iwaniuk, A. N. and J. E. Nelson. 2003. Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can. J. Zoolog. 81:1913-1928.

Jetz, W., G. Thomas, J. Joy, K. Hartmann and A. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Lashley, K. S. 1949. Persistent problems in the evolution of mind. Q. Rev. Biol. 24:28-42.

Lefebvre, L., S. M. Reader and D. Sol. 2004. Brains, innovations and evolution in birds and primates. Brain Behav. Evolut. 63:233-246.

Lefebvre, L. and D. Sol. 2008. Brains, lifestyles and cognition: are there general trends? Brain Behav. Evolut. 72:135-144.

Lefebvre, L. 2013. Brains, innovations, tools and cultural transmission in birds, non-human primates, and fossil hominins. Front. Hum. Neurosci. 7:10-3389.

Mazerolle, M. J. 2015. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3. http://CRAN.R-project.org/package=AICcmodavg.

McGuire, L. P. and J. M. Ratcliffe. 2011. Light enough to travel: migratory bats have smaller brains, but not larger hippocampi, than sedentary species. Biol. Lett. 7:233-236.

Mitchell, T. D. and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int. J. Climatol., 25:693-712.

Newton, I. 2008. The ecology of bird migration. Academic Press, London, U.K.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., and Pearse, W. 2014. caper: Comparative Analyses of Phylogenetics and Evolution in R, R package version 0.5.2; 2013. http://CRAN.R-project.org/package=caper

Piersma, T. and Å. Lindström. 1997. Rapid reversible changes in organ size as a component of adaptive behaviour. Trends Ecol. Evol. 12:134-138.

Pravosudov, V. V. and N. S. Clayton. 2002. A test of the adaptive specialization hypothesis: population differences in caching, memory, and the hippocampus in black-capped chickadees (*Poecile atricapilla*). Behav. Neurosci. 116:515.

Pravosudov, V. V., K. Sanford and T. P. Hahn. 2007. On the evolution of brain size in relation to migratory behaviour in birds. Anim. Behav. 73:535–539.

R Core Team. 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reader, S. M. and K. N. Laland. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proc. Natl. Acad. Sci. USA 99:4436–4441.

Roth, T. C. and V. V. Pravosudov. 2009. Hippocampal volumes and neuron numbers increase along a gradient of environmental harshness: a large-scale comparison. Proc. R. Soc. Lond. B 276:401-405.

Roth, T. C., L. D. LaDage and V. V. Pravosudov. 2011. Variation in hippocampal morphology along an environmental gradient: controlling for the effects of day length. Proc. R. Soc. Lond. B rspb20102585.

Rothman, K. J. 1990. No adjustments are needed for multiple comparisons. Epidemiology. 1:43–46.

Rothman, K. J. 2014 Six persistent research misconceptions. J Gen Int Med. 29:1060-1064.

Rubolini, D., A. Liker, L. Z. Garamszegi, A. P. Møller and N. Saino. 2015. Using the BirdTree. org website to obtain robust phylogenies for avian comparative studies: A primer. Current Zool. 61:959-965.

Sayol, F., L. Lefebvre and D. Sol. 2016. Relative Brain Size and Its Relation with the Associative Pallium in Birds. Brain Behav. Evolut. 87:69-77.

Schuck-Paim, C., W. J. Alonso and E. B. Ottoni. 2008. Cognition in an ever-changing world: Climatic variability is associated with brain size in neotropical parrots. Brain Behav. Evolut. 71:200-215.

Sol, D., N. Garcia, A. Iwaniuk, K. Davis, A. Meade, W. A. Boyle and T. Székely. 2010. Evolutionary divergence in brain size between migratory and resident birds. PloS ONE 5:e9617.

Sol, D., L. Lefebvre and J. D. Rodríguez-Teijeiro. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proc. R. Soc. Lond. B 272:1433–1441.

Sol, D., T. Székely, A. Liker, L. Lefebvre. 2007. Big-brained birds survive better in nature. Proc. R.

570 Soc. Lond. B 274:763-769.
571 Sol, D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biol. Lett.
572 5:130-133.
573 Timmermans, S., L. Lefebvre, D. Boire and P. Basu. 2000. Relative size of the hyperstriatum ventrale is
574 the best predictor of feeding innovation rate in birds. Brain Behav. Evolut. 56:196-203.
575 Vágási, C. I., P. L. Pap, O. Vincze, G. Osváth, J. Erritzøe and A. P. Møller. 2016. Morphological
576 adaptations to migration in birds. Evol. Biol. 43: 48-59.
577 Vincze, O., I. C. Vágási, P. L. Pap, G. Osváth and A. P. Møller. 2015. Brain regions associated with
578 visual cues are important for bird migration. Biol. Lett. 11:20150678.
579 Winkler, H., B. Leisler and G. Bernroider. 2004. Ecological constraints on the evolution of avian brains.
580 J. Ornithol. 145:238-244.

Table 1. Models exploring the relationship between brain size and migration distance in birds with different migratory strategies. Each row represents a separate model. All models include body mass as covariate (effect of body mass not shown).The first column provides the criteria used to define the species pool for each model. t- and P-values shown here are weighted averages over 100 PGLS models with different phylogenetic trees. The sign of t value indicates the direction of the association, while their value show the strength of association. Results from analyses of the entire taxonomic range and restricted analyses of passerines are provided.

	Entire species pool				**Passerine species**			
Migration distance restriction	**n**	**t-value**	**P-value**	**R^2**	**n**	**t-value**	**P-value**	**R^2**
No restriction	1466	-5.37	<0.0001	0.89	610	-6.44	<0.0001	0.90
> 0 km	529	-3.11	0.0022	0.90	189	-4.22	<0.0001	0.92
> 500 km	387	-3.60	0.0004	0.90	143	-4.49	<0.0001	0.92
> 1,000 km	326	-2.74	0.0067	0.92	119	-3.82	0.0002	0.93
> 2,000 km	233	-3.60	0.0004	0.92	78	-3.42	0.0010	0.92
> 0 & < 500km	142	2.21	0.0319	0.92	46	2.47	0.0179	0.95
> 500 & < 1,000km	61	0.78	0.4415	0.87	24	0.48	0.6434	0.93
> 2,000 km & tropical wintering	146	-3.32	0.0012	0.92	58	-3.34	0.0015	0.90

589 **Table 2.** Models exploring the relationship between brain size and non-breeding minimum temperature, seasonality or non-breeding latitude
590 in birds with different migratory strategies. Each row represents a separate model. All models include body mass as covariate (effect of body
591 mass not shown). The first column provides the criteria used to define the species pool each model was based on. Where two sample sizes
592 are given, the first refers to the minimum temperate and the seasonality models, while the second to the non-breeding latitude model. t- and
593 P-values shown here are weighted averages over 100 PGLS models with different phylogenetic trees. The sign of t value indicates the
594 direction of the association, while their value show the strength of association. Results from analyses of the entire taxonomic range and
595 restricted analyses of passerines are provided.
596

		Non-breeding minimal temperature			**Seasonality**			**Non-breeding latitude**		
Migration distance restriction	**n**	**t-value**	**P-value**	**R^2**	**t-value**	**P-value**	**R^2**	**t-value**	**P-value**	**R^2**
Entire species pool										
0 km	934/937	-2.55	0.0134	0.89	0.53	0.6029	0.89	0.34	0.7274	0.89
< 500 km	1076/1079	-3.50	0.0007	0.89	1.38	0.1794	0.89	1.27	0.2153	0.89
< 1,000 km	1137/1140	-3.57	0.0005	0.89	1.24	0.2235	0.89	1.45	0.1572	0.89
0 > & < 500km	142	-4.14	0.0001	0.93	2.84	0.0060	0.93	3.84	0.0002	0.93
> 500 & < 1,000km	61	-1.83	0.0725	0.88	1.99	0.0524	0.88	2.17	0.0344	0.88
Passerines										
0 km	421	-2.77	0.0062	0.90	0.84	0.4021	0.90	1.79	0.0752	0.90
< 500 km	467	-3.70	0.0003	0.90	1.43	0.1556	0.90	2.42	0.0162	0.90
< 1,000 km	491	-3.27	0.0012	0.90	0.75	0.4598	0.89	2.10	0.0367	0.89
0 > & < 500km	46	-4.47	0.0001	0.97	3.36	0.0017	0.96	3.42	0.0014	0.96
> 500 & < 1,000km	24	-1.07	0.2974	0.94	0.47	0.6453	0.94	1.36	0.1871	0.94

597

FIGURE LEGENDS

Figure 1. Map illustrating geographic data coverage. Orange circles represent the geometric centroid of the breeding areas, green pluses represent the geometric centroids of the wintering grounds of the studied species.

Figure 2. Association between migration distance and body-mass controlled residual brain weight in the entire species list (A), in species with migration distance between 0 and 1,000 km (B), and in species with migration distance over 2,000 km (C). Figures D-E-F show the same for passerines only. Note that figures are based on raw data points, therefore much of the variation can be accounted to phylogenetic effects.

Figure 3. The association between non-breeding minimum temperature and body-mass controlled residual brain weight in fully resident species (A), in species with migration distance between 0 and 500 km (B), and in species with migration distance between 500 and 1,000 km (C). Figures D-E-F show the same for passerines only. Note that figures are based on raw data points, therefore much of the variation can be accounted for by phylogenetic effects (e.g. green filled circles on figure 3A,B,C denote species from the *Galliformes* bird order).